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DISTANCE OF DISPERSAL BY PRAIRIE DEERMICE FROM BIRTHPLACES TO BREEDING SITES

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INTRODUCTION

THE dispersal movements which in each generation carry young animals from their birthplaces to the sites where they themselves reproduce have many important biological consequences. This dispersal of the individuals aids the young to find unoccupied habitats suitable for the species, tends toward a more even utilization of the habitat resources, reduces the likelihood of inbreeding, promotes the mixing of hereditary factors throughout the whole population, and furthers the spread of new genes.

In the present study an attempt was made to treat statistically the distance traveled in dispersal movements by individuals born into a local society of prairie deermice (Peromyscus maniculatus bairdii). The area chosen is on the Edwin S. George Reserve near Pinckney, Livingston County, in southern Michigan (Map 1). The field data were gathered by the junior author under the direction of the senior author. The senior author is responsible for the statistical analysis. The two authors have co-operated in the preparation of the manuscript and are jointly responsible for the conclusions.

METHODS OF STUDY

The deermice considered in this study were marked as young individuals while in the nest boxes provided. Many of these mice were later observed, in breeding condition or associated with young, either in the nest boxes in which they were first noted or in other boxes some distance away (Howard, 1949). The distance of dispersal was taken to be that of a direct line from the nest box in which an animal was born, or was first discovered at less than weaning age, to the box in which it was afterward found in breeding condition. Records of individuals which were born during late fall and wintered over at their birthplaces before becoming sexually mature or dispersing, were not included unless the mice were observed again after the usual time of breeding and dispersal in the spring, here taken to be March 19 or later. A few records of dispersal distance were obtained from live traps set in the same fields as the nest boxes.

Although the measurements of dispersal distance (Table I) were made in a straight line between the points concerned, the actual dispersal travel of each individual was almost certainly not in a direct line. Our measurements apply, then, only to the distances between the natal sites and the adult breeding sites; they do not apply to the actual distances traveled by individuals.

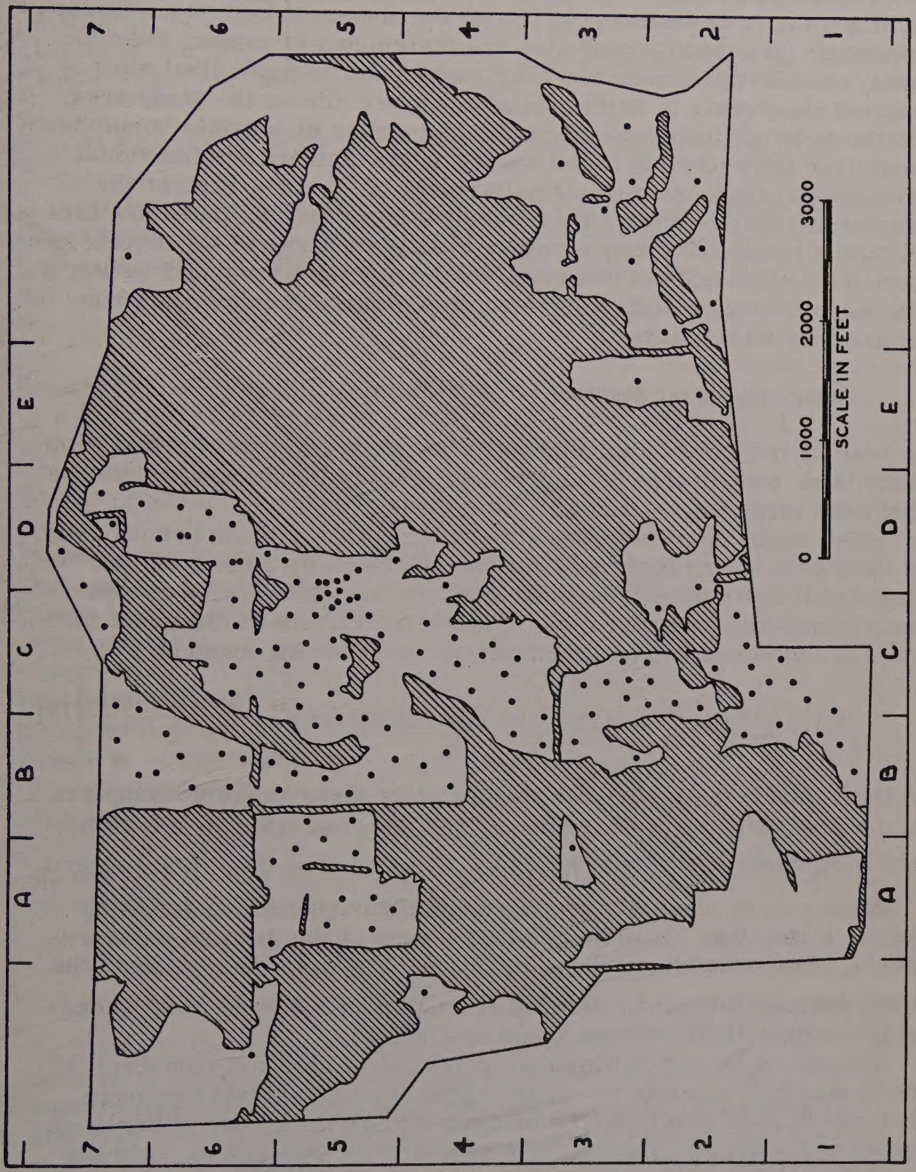
The nest boxes used were rarely set closer than 200 feet, although some of the live traps were more closely spaced. We have, consequently, no record of less than 200 feet for transfer of homesite which included evidence of breeding activity. All measurements of dispersal distance have been rounded to the nearest 50 feet.

Certain individuals became sexually mature and produced offspring in the same nest box in which they themselves had been born. The dispersal distance for such an individual was, of course, zero. A few individuals changed their homesites one or more times after they had become sexually mature, which necessitated calculation of a mean distance of dispersal for them.

The distances moved by individuals which were not yet sexually mature when last seen have not been included in these calculations. Those individuals which dispersed to the greatest distances probably moved entirely beyond the area covered by traps. As a result, the maximum distances of dispersal and the mean distances reported here are undoubtedly too short.

STATISTICAL TREATMENT OF DISPERSAL DISTANCES

The distance that an individual mammal moves in dispersal from birthplace to breeding site may be affected by several possible factors. In order to treat statistically measurements of individual dispersal distances, it is necessary to make certain simplifying assumptions, namely, that (1) each individual animal is free to move away from its birthplace



MAP 1. The Edwin S. George Reserve. The grassland areas are unshaded and locations of the nest boxes are marked by dots.

in any direction without encountering any serious barrier to his movements; (2) there is no competition for homesites between the several individuals of the species; (3) the distance that any individual moves in dispersal is dependent solely upon the chance of finding a suitable homesite; (4) suitable homesites are distributed at random over the area; and (5) the animals are fully mobile and no more likely to remain at their place of birth than at any other site on the study area. On the basis of these assumptions, the number of possible homesites increases in proportion to the square of the distance the individual moves away from the birthplace (Wright, 1943). The farther the animal moves the greater the number of opportunities there are for it to obtain a suitable home. Since the square roots of the distances moved by individuals in dispersal should approach a normal curve, the mean dispersal distance for a group of similar individuals can be given by the formula:

$$\text{Mean dispersal distance} = \left[(S\sqrt{d})/n\right]^2, \qquad (1)$$

in which S indicates "the sum of," d the distance moved by any given individual from birthplace to breeding site, and n the number of individuals included in calculating this mean.

After initial dispersal some deermice did not remain permanently at the site at which they had first become sexually mature or had first bred, but moved to another site. In fact, a few mice moved their homesites several times. The mean distance of dispersal for such an individual can be estimated by the following formula:

$$\text{Mean dispersal distance for any individual} = \left[\frac{\sqrt{d}_{max} \pm \sqrt{d}_{min}}{2}\right]^2 \qquad (2)$$

In this formula d_{max} indicates the greatest distance from birthplace to the homesite, d_{min} the least. If an individual takes up one of his adult residences exactly at his place of birth, then d_{min} will be zero.

When square roots are averaged and then squared the resulting figure is less than the arithmetical average of the original measurements. For example, if d_{max} is 200 feet and d_{min} is zero feet, the mean dispersal distance obtained from Formula 2 is 50 feet, whereas the arithmetical average would be 100 feet.

In those instances in which an individual is known to have bred at more than two separate sites, it is possible to calculate the mean distance of each site from the birthplace. As knowledge of the movements and breeding sites of these deermice is incomplete, only the greatest and least distances obtained for each individual were considered in calculating the mean dispersal distance.

In our statistical treatment of the data of dispersal we worked mostly with the square roots of the distances moved by the various individuals. From these square roots the variances of the means and other related statistics may be calculated. If a statement in terms of the original units of measurement is desired, then each square-root statistic must be squared.

FACTORS THAT MAY AFFECT DISPERSAL DISTANCE

Among the factors that may affect dispersal movements of prairie deermice, we shall consider chiefly barriers, population density, age and season of dispersal, home-range habit, and difference in sex.

Barriers to Dispersal

The population of deermice lived in a group of grassy fields interspersed between patches of oak-hickory woods (Map 1). The fields have regenerated since the native forest was cleared many years ago. After clearing, the land was cultivated for a time, then abandoned.

Prairie deermice are restricted to open fields and do not live in forest. Since most of the fields on the George Reserve are interconnected, the deermice were able to pass more or less directly from field to field. The areas of forest, nevertheless, may constitute partial or, in certain directions, perhaps complete barriers to movements. A mouse born in a nest near the edge of a field would not be equally free to disperse in any direction. In calculating the dispersal distances of each animal an allowance should properly be made to compensate for the presence of these barriers to dispersal. In our calculations no such account has been taken of the possible limitation of dispersal distances by forest barriers. We know so little about the actual effect of these wooded patches on deermouse dispersal that any allowance for this factor would have had to be based largely on unproved assumptions.

Density of Population

There is little information available concerning the effects which density of population has upon the dispersal of deermice. It is not known whether a greater proportion of the maturing offspring will disperse under crowded conditions than when population density is at a low level. Furthermore, it is not known if the dispersing individuals will travel greater distances when the population is dense than they will when it is sparse. Deermice tend to distribute their home ranges so as to occupy a habitat fairly uniformly. When Blair (1940) removed most of the deermouse population from an area of

4.46 acres, numerous individuals from the surrounding area promptly moved into the depopulated habitat, with which they were probably already acquainted. In another instance, in which extra artificial homes had been provided (Howard, 1949: 24), additional deermice were not attracted into an already well-populated area.

Age and Season of Dispersal

Observations by Howard (1949: 22) seem to demonstrate that the dispersal of prairie deermice takes place just prior to the time when they become sexually mature. Up to the approach of sexual maturity the young remain within the home range of their parents.

Deermice that are born between March and early September mature sexually the same season. Of these, the mice that dispersed did so when only 4.5 to 7.0 weeks of age. Individuals born during the latter part of the breeding season, that is from the middle of September to early November, do not mature sexually until the following spring, when they are from 14 to 25 weeks of age, and these young mice often remain with their parents over the winter. Consequently, each spring some of the dispersing deermice would have been taken to be old breeding animals, since they were five or six months of age, had it not been known that they were becoming sexually active for the first time.

The data obtained give no indication that the distance of dispersal is affected by the age of the individuals or by the season of the year in which the dispersal movements occur.

Home-range Habit

Each prairie deermouse, like members of most other species of mammals, lives within a restricted area, which constitutes its home range (Blair, 1940). It would be helpful to be able to distinguish between those movements of an individual which are included within his usual home range and the movements which constitute dispersal and subsequent establishment of a new home range.

By spacing live traps on the George Reserve in a checkerboard pattern and retrapping marked individuals, Blair (1942) estimated that home ranges of adult male prairie deermice average 0.77 acre and those of adult females, 0.63 acre. The largest home range occupied over a period of a month was 1.67 acres for a male and 2.29 acres for a female (Blair, 1940). A home range covering 2.29 acres (the maximum area recorded by Blair), if circular in shape, would be only 236 feet in diameter. We agree with Blair that his method of study results in too small an estimate of home-range area, because each individual tends to be trapped each night before he has traveled from his homesite to the outer limits of his range.

Studies of prairie deermice by Howard (1949) demonstrate that many individuals actually have home ranges which are more than 236 feet in diameter. Tracks in the snow show that they may travel for some distance from the nest box in which they are living. Although they seldom travel more than 400 feet in a straight line from their homesites, one mouse went as far as 800 feet. Each animal usually returned by almost exactly the same route as that used when going away from his home nest box. In winter it was not unusual for an entire aggregation (all the mice living in one box) to move as much as 500 feet and take up a new residence in a different nest box, but one presumably still within the same home range. Just before producing a new litter a female may move as much as 500 feet to a new box, leaving the old litter in the previous nest. During the live trapping, carried out in connection with this study, one female was caught 250 feet from the nest box containing her week-old litter, which she nursed again after her release. A male (with one hind leg missing) was live-trapped 300 feet from his home nest box. A cache of 65 acorns was stored in a nest box which was 225 feet distant from the nearest branch of an oak tree. A male and his four offspring were trapped together in a single-catch live trap at night, 300 feet from the nest which the young had occupied the previous day. Still another deermouse was trapped 350 feet from the nest box which was his home.

As has Blair pointed out, the homesite of a prairie deermouse is not always in the middle of its home range. Further, the frequency with which an individual visits the several sections of his home range, and also the size, shape, and permanency of the home range, is undoubtedly affected by sex, age, season, presence of food, local physical conditions of the habitat, local density of the deermouse population, presence of predators, and other factors.

Ascertainment of the exact boundaries of the home range of a particular individual is difficult. Use of nest boxes alone will not suffice. We are, therefore, unable to distinguish in these records between changes of residence within a home range by a prairie deermouse and those dispersal movements which would require him to set up a new home range or at least to modify his former home-range boundaries.

Difference in Sex

In the population studied, the males dispersed farther on the average from their birthplaces than did the females. The mean dispersal distance for the males is 339 feet (square root = 18.41 ± 1.84) and for the females only 188 feet (square root = 13.71 ± 1.76). The difference between the square roots of the two means is not significant.

Part of the difference between the dispersal distances traveled by the males and females is due to there having been a larger proportion of females than males which remained at their birthplaces to breed. Many mice of both sexes came into breeding condition within the home ranges in which they were born. Some females are known to have produced young in the same nest boxes in which they themselves were born. Twenty-seven (38 per cent) of the females and eighteen (28 per cent) of the males came into breeding condition within their natal home ranges and were not known to have dispersed from their homesites. Five other females and four other males were presumed to have bred within their natal ranges, although they later dispersed varying distances and came to occupy new homesites.

If the 27 females and 18 males which did not disperse away from their birthplaces are not considered, then the mean dispersal distance of the remaining individuals is 489 feet for the females and 685 feet for the males. Again the difference between the square roots of the distances is not significant.

Previous studies by Blair (1940) on the George Reserve have shown that male prairie deermice which shift their natal ranges, travel farther than do females before establishing new homes. The distance average moved by 12 males was 1168 feet, whereas that moved by 18 females was only 758 feet. These are arithmetic averages and are not to be compared with the mean dispersal distances calculated according to the formulas given above. Also, these averages are based only on the animals known to have moved their home ranges and are, consequently, greater than if account had been taken of those that did not move from their birthplaces. Nevertheless, Blair's data suggest that males do, when they disperse away from their birthplaces, tend to move farther away than females.

Males seem to disperse farther than females, yet some females dispersed very considerable distances. The longest dispersal records which we obtained were made by females, four of which traveled 3300, 3200, 3200, and 2900 feet, respectively. The four males which made the greatest dispersal records, traveled only 2900, 2450, 2450, and 1950 feet, respectively.

Evidence concerning the length of dispersal distances of males and females is, therefore, somewhat contradictory. Our records and those of Blair indicate that males, on the average, disperse farther than females. In our records, however, the difference in dispersal distance between males and females is not significant. A greater proportion of males than of females disperse away from their birthplaces. Three females, however, dispersed to greater distances than any of the males. A larger body of data than we now possess might demonstrate that there is a difference in dispersal pattern between males and females, but at present no such difference has been proved.

Additional Factors

Numerous factors in addition to those discussed above doubtless affect the dispersal movements of prairie deermice, such as (1) local abundance of food and the presence of favorable conditions in the physical habitat; (2) unfavorable weather at the time of dispersal movements, which might limit distances traveled before taking up a residence; (3) attacks by predators or by quarrelsome individuals of nonpredaceous species; (4) an innate physiologic stimulus which might motivate certain individuals but not others to leave their birthplaces; and (5) hereditary variation in the other reactions among individuals. The spacing of nest boxes probably influences the distribution of suitable homesites, and may have affected the distances of dispersal recorded for the population studied.

VARIABILITY IN DISTANCES OF DISPERSAL

The curves of dispersal distance (Figs. 1 and 3) show that prairie deermice do not disperse at random. The curves for the square roots of the individual dispersal distances are strongly skewed to the left. A large part of this skewness can be attributed to the 38 per cent of females and 28 per cent of males which did not disperse away from their natal homesites. Even if these stay-at-home individuals are ignored, the dispersal curves, both for females and for males, are still not normal. More individuals dispersed long distances than would be expected on the basis of chance.

There are several possible explanations for the greater distances of dispersal of certain individuals than would be expected on the basis of chance alone. Barriers to dispersal may prevent travel being equally easy in all directions from the birthplace; suitable homesites may not be everywhere equally abundant, so that a dispersing individual must sometimes wander considerably before finding a satisfactory location; or most nearby suitable homesites may already be occupied, because of a local crowding of the population. Our data are not sufficient to evaluate these and other possible factors that might affect the dispersal distances of individual prairie deermice, or even to demonstrate that any one of them is actually operative.

Once a young prairie deermouse has bred at a particular site, he is likely to remain in that vicinity for life, as he has established a home range there. For most individuals dispersal occurs only once, usually just before breeding. Several mice, according to our records, however, gave evidence of breeding at more than one site. In Table I are listed eleven females (15 per cent of all females) and sixteen males (25 per cent of all males) which differ in their maximum and minimum dispersal distances, an indication that these individuals changed their breeding sites at least once. The maximum

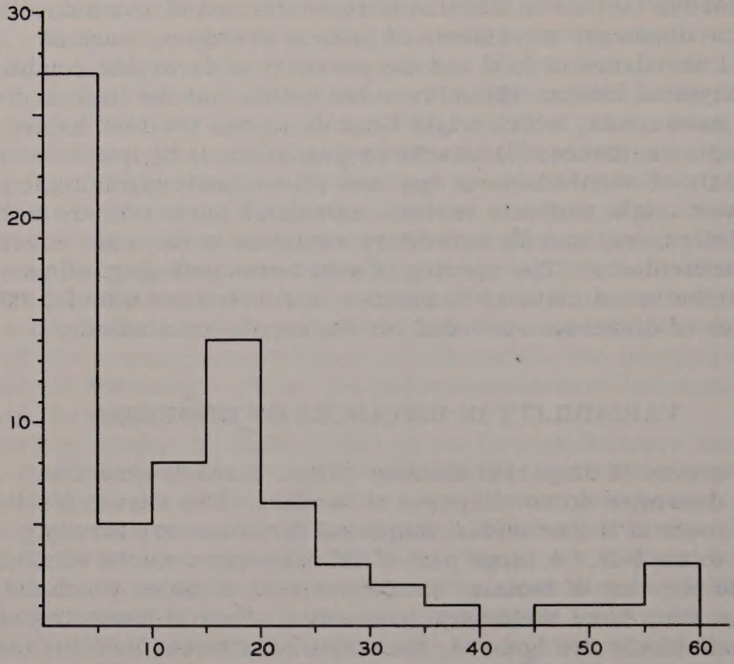


FIG. 1. Frequency polygon for the square roots of the dispersal distances (in feet) of 71 female prairie deermice.

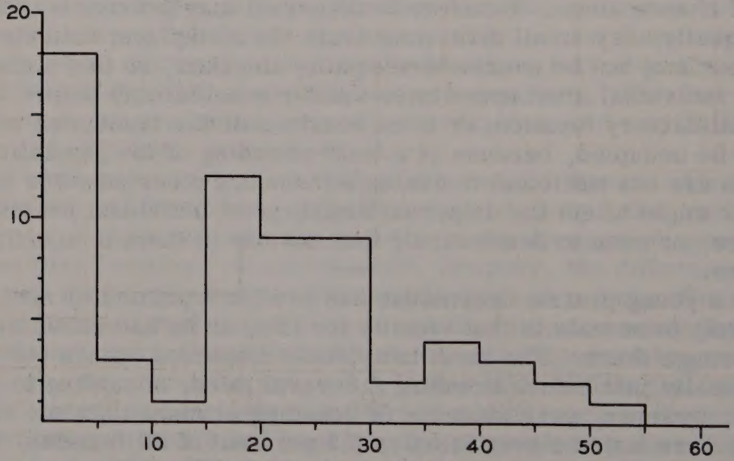


FIG. 2. Frequency polygon for the square roots of the dispersal distances (in feet) of 64 male prairie deermice.

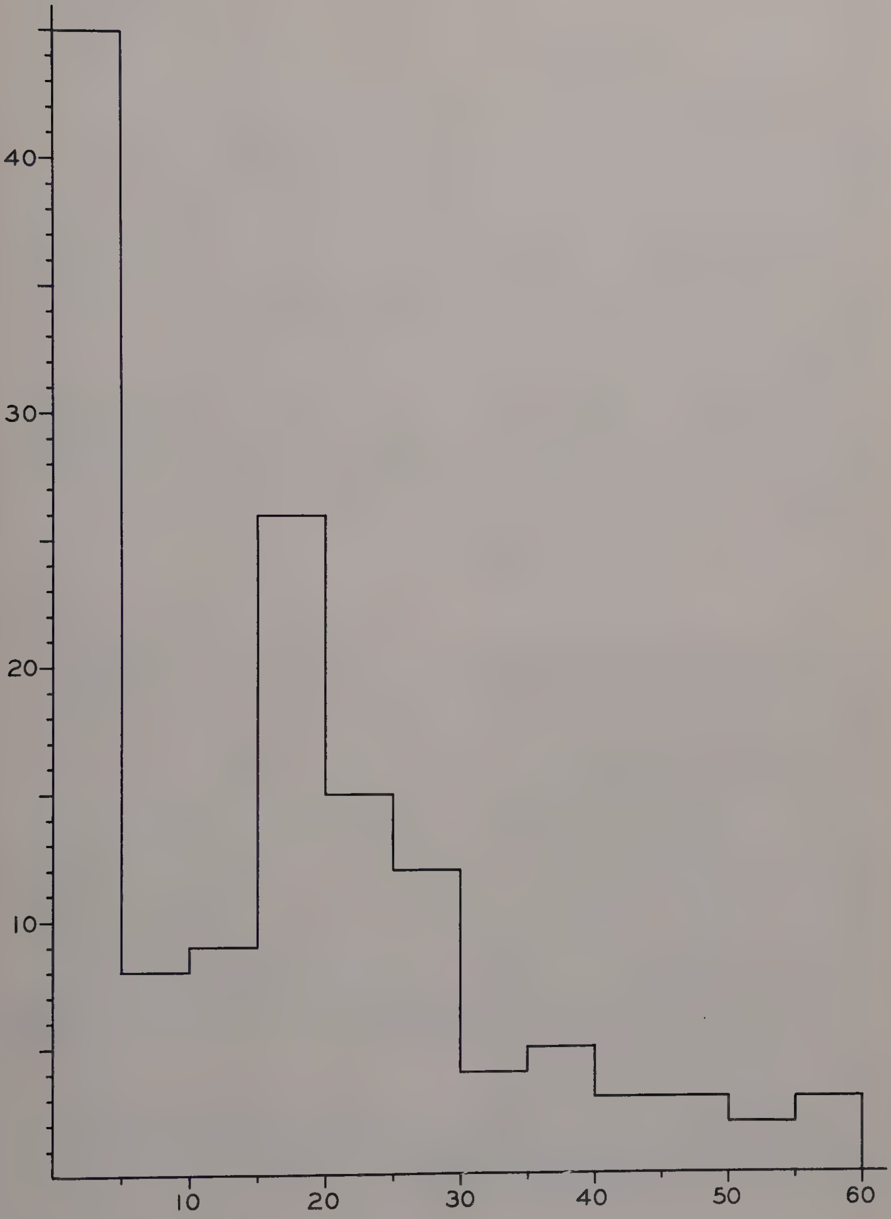


FIG. 3. Frequency polygon for the square roots of the dispersal distances (in feet) of 135 male and female prairie deermice.

distance between any two breeding sites used by the same female (B80) was 600 feet, but two males (B65 and B88) each moved 1450 feet during one breeding season. Some of these changes in breeding site may only be movement within the boundaries of a single home range, but others certainly involved changes in home range. One (B88) of the two males was reported from five nest boxes during the breeding season. Such behavior is not unusual, but all the movements of this individual between nest boxes happened to be in the same direction, so that his total dispersal distance of 1450 feet considerably exceeds the average. Another male (not included in Table I) was recorded 2050 feet from his birthplace, but one week later had returned, presumably without breeding at the distant site. This male was the only individual which is known to have traveled any considerable distance away and then returned to his birthplace.

Because of the strongly skewed curves for dispersal distances traveled by these prairie deermice and because of the many factors known to influence their distance of dispersal, no statement of the variance of these measurements has been presented here. The range of variation in the distances to which these mice disperse, however, are given in Table I and in Figures 1 and 2.

SUMMARY

Measurements of the distances that young prairie deermice disperse from their birthplaces to the sites at which they themselves breed are presented for 71 females and 64 males. Movements of marked individuals were traced by means of nest boxes distributed over a regenerating grassy field in southern Michigan.

For the statistical treatment of the measurements of dispersal distance, the square-root transformation was used. Dispersal usually occurs just prior to breeding, but 38 per cent of the females and 28 per cent of the males remained within their natal home ranges to breed. The mean dispersal distance was 188 feet for females and 339 feet for males, but this difference between the sexes is not statistically significant. The maximum dispersal distance was 3300 feet for a female (A211) and 2900 feet for a male (B311). A majority of the individuals remained permanently at any site at which they had once bred, but 15 per cent of the females and 25 per cent of the males bred at more than one site.

The distances which prairie deermice travel in their individual dispersal movements are nonrandom in distribution, but we are unable to evaluate the influence of each of the possible genetic and ecologic factors which may affect dispersal.

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TABLE I

DISPERSAL DISTANCES OF INDIVIDUAL DEERMICE

Distance in direct line from birthplace, or from nest box in which the individual was observed before weaning, to site or sites where he bred or came into breeding condition.

Mouse Number	Dispersal Distance		
	Greatest d_{max}	Least d_{min}	Mean $\left[\frac{\sqrt{d_{max}}\pm\sqrt{d_{min}}}{2}\right]^2$
	Females		
237 ...	800	650	723
341 ...	300	0	75
A96 ...	1900	1900	1900
A102 ...	600	600	600
A131 ...	350	350	350
A136 ...	800	800	800
A201 ...	0	0	0
A203 ...	0	0	0
A211 ...	3300	3300	3300
A229 ...	350	300	325
A233 ...	200	200	200
A237 ...	0	0	0
A241 ...	0	0	0
A244 ...	0	0	0
A250 ...	200	200	200
A257 ...	0	0	0
A273 ...	350	200	270
A278 ...	300	0	75
A294 ...	0	0	0
A306 ...	250	0	63
A312 ...	250	250	250
A318 ...	0	0	0
A320 ...	250	250	250
A330 ...	1250	1250	1250
A344 ...	500	400	449
A350 ...	200	200	200
A372 ...	3200	3200	3200
A380 ...	0	0	0
B1 ...	0	0	0
B7 ...	900	900	900
B16 ...	950	950	950
B21 ...	0	0	0
B23 ...	350	350	350
B29 ...	200	200	200
B52 ...	250	250	250
B53 ...	350	350	350
B58 ...	200	200	200
B74 ...	350	0	88
B78 ...	0	0	0
B80 ...	600	0	150
B82 ...	600	350	467
B92 ...	0	0	0
B94 ...	800	300	520
B95 ...	250	0	63
B97 ...	0	0	0
B99 ...	0	0	0
B111 ...	0	0	0
B112 ...	0	0	0
B120 ...	250	250	250
B124 ...	250	250	250
B127 ...	500	500	500
B130 ...	250	250	250
B133 ...	0	0	0
B135 ...	2900	2900	2900
B136 ...	0	0	0
B162 ...	350	350	350
B205 ...	0	0	0
B313 ...	450	450	450
B329 ...	0	0	0
B339 ...	0	0	0
B348 ...	200	200	200
B358 ...	300	300	300
B363 ...	0	0	0
C19 ...	200	200	200
C31 ...	0	0	0
C32 ...	0	0	0
C36 ...	650	650	650
C51 ...	300	300	300
C52 ...	0	0	0
C87 ...	0	0	0
L6 ...	3200	3200	3200
	Males		
342 ...	300	0	75
343 ...	850	300	540
347 ...	350	0	88
A97 ...	550	550	550
A99 ...	1550	1350	1448

Table I - (Cont.)

Mouse Number	Dispersal Distance			Mouse Number	Dispersal Distance		
	Greatest d_{max}	Least d_{min}	Mean $\left[\frac{\sqrt{d_{max}} \pm \sqrt{d_{min}}}{2}\right]^2$		Greatest d_{max}	Least d_{min}	Mean $\left[\frac{\sqrt{d_{max}} \pm \sqrt{d_{min}}}{2}\right]^2$
A108 ...	200	0	50	B54 ...	250	250	250
A120 ...	1650	1650	1650	B56 ...	850	700	773
A122 ...	1950	1950	1950	B65 ...	1450	200	682
A126 ...	650	650	650	B66 ...	700	700	700
A202 ...	250	250	250	B71 ...	0	0	0
A204 ...	450	0	112	B72 ...	0	0	0
A206 ...	0	0	0	B75 ...	0	0	0
A208 ...	250	250	250	B87 ...	450	450	450
A209 ...	350	350	350	B88 ...	1450	300	767
A216 ...	300	300	300	B102 ...	0	0	0
A221 ...	0	0	0	B107 ...	250	250	250
A223 ...	300	200	247	B164 ...	1000	750	871
A231 ...	550	550	550	B165 ...	1250	1250	1250
A248 ...	900	900	900	B169 ...	900	550	715
A295 ...	450	450	450	B178 ...	0	0	0
A297 ...	250	250	250	B187 ...	500	500	500
A311 ...	750	500	619	B204 ...	350	350	350
A319 ...	650	650	650	B208 ...	450	250	343
A339 ...	850	450	634	B236 ...	0	0	0
A340 ...	1200	1200	1200	B239 ...	0	0	0
A367 ...	0	0	0	B263 ...	450	250	343
A378 ...	450	450	450	B279 ...	0	0	0
A391 ...	0	0	0	B331 ...	2900	2900	2900
B10 ...	0	0	0	B337 ...	2450	2450	2450
B15 ...	550	550	550	B352 ...	1300	1300	1300
B18 ...	0	0	0	B354 ...	0	0	0
B25 ...	0	0	0	B355 ...	0	0	0
B26 ...	0	0	0	B356 ...	300	300	300
B35 ...	1450	1450	1450	C46 ...	2450	2450	2450
				01 ...	1900	1900	1900